**State-Transition Manuscript Draft**

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**Introduction**

Global climate change is forecast to produce dramatic shifts in the frequency and magnitude of extreme climate events across ecosystems worldwide. In many systems, increased drought severity, wildfire intensity, and flooding are expected to significantly impact ecosystem structure and function.

To better understand and adapt to these pressures, ecologists have increasingly focused on the concept of resilience – the ability of an ecosystem to resist change and self-reorganize following perturbation (Folke 2006). Resilience thinking has proven valuable when applied to systems that exhibit complex, nonlinear transitions between multiple states, and are increasingly used to guide management in a wide range of circumstances (Scheffer et al. 2001, Smith 2011, Angeler and Allen 2016).

In particular, resilience thinking has provided a strong conceptual basis for the management of arid and semi-arid rangelands, where traditional range models based on successional processes often fail to capture vegetation dynamics (Jackson and Bartolome 2002). Instead, range managers in these systems have turned to state and transition models (STMs), which describe plant community turnover as a set of transitions between discrete vegetation states. This approach attempts to recognize the complex interactions that govern vegetation composition by describing both the resilience of each individual state type and the many factors -- such as environmental variation and management actions – that guide transitions between them.

**California Annual Grasslands**

California grasslands have long been a focal system in the study of nonequilibrium dynamics in plant communities. Readily shifting between dominant vegetation groups (George et al. 1992), California grasslands are theorized to exhibit high sensitivity to interannual climatic variation (Hobbs and Mooney 1995, Hobbs et al. 2007), non-hierarchical competitive dynamics (Uricchio et al. 2018), and strong priority effects (Young et al. 2014). Collectively, these mechanisms prevent predictable convergence to a single community type, irrespective of grazing or disturbance history.

In a state-transition perspective, California grassland vegetation are often partitioned into several distinct groups, including those based on functional type (grasses, forbs, and legumes) and provenance (native and exotic species). Distinctions are most frequently made between

1) Naturalized exotic annual grasses that now compose a majority of vegetation in California’s grassland ecosystems; 2) Native perennial grasses and forbs thought to once cover much of the state’s grassland habitat; 3) A set of highly invasive annual grasses that are rapidly expanding throughout California rangelands.

Past work has established general patterns in group life history strategy that correlate with colonization ability, invasion resistance, and response to climatic variation (Corbin et al. 2007, Harpole et al. 2007, Abraham et al. 2009). Exotic and native grasses exhibit pronounced differences in seed physiology, growth habit, and fecundity.

Large-seeded exotic annuals germinate rapidly with the onset of winter rains and invest heavily in reproduction before senescence, producing germinable seed densities up to 100,000 seeds/m2 (Bartolome 1979). Native grasses, on the other hand, often produce far fewer seeds of much lower mass that may fail to compete with annual grasses at early life stages. However, once established, hardy perennials are characterized by low mortality and long-term persistence without active disturbance (Seabloom et al. 2003). Similar to exotic annuals, invasive grasses produce seeds in high densities, though exhibit a later phenology and pronounced litter feedbacks that may inhibit growth of new colonists (Young 1992).

Through interaction with these different life history strategies, seasonal patterns of precipitation and temperature can exert considerable control over productivity and community composition in California grasslands (Pitt and Heady 1978, Reever Morghan et al. 2007). For example, periodic droughts early in the growing season are thought to result in significant mortality of annual grasses, while late-season rains may favor growth of late-season invasive species.

Recent, large-scale disturbances in the form of a historic drought and widespread wildfires have emphasized the need to predict vegetation dynamics as communities respond to these events. Current climate projections emphasize increased duration and intensity of drought events in California which may act as critical tipping points in grassland ecosystems (Shaw et al. 2009, Pierce et al. 2012, Prugh et al. 2018).

**Justification**

While primarily used as descriptive tools, state-transition frameworks employed by managers in California rangelands may also serve as a framework for the statistical analysis of vegetation dynamics. To date, attempts to incorporate state-transition concepts into statistical analysis have been limited in number, but effective in capturing community turnover in arid and semi-arid systems. As a complement to existing management tools, attempts to quantitatively generate state-transition models have been used to evaluate spatial and temporal variation in grassland vegetation, as well as refine predictions made by expert-derived state-transition models. Most recently, Bagchi et al. (2012) and Stein et al. (2016) used this method to explore cheatgrass spread and resistance in the American Great Basin and grazing effects on vegetation dynamics in California rangelands, respectively.

Shared among all quantitative state-transition models is the application of algorithmic clustering to partition plant community variation. By describing vegetation as a set of discrete “states”, partitioning methods establish correlated changes in abundance among species groups. These group associations may be used to determine similarities in performance within species pools, as well as quantify the effect of potential triggers that may prompt transition between different state types.

This methodology is highly adaptable to a wide range of systems and purposes. Algorithmic clustering provides a defined rationale for the establishment of vegetation states that may complement existing state-transition models constructed from long-term qualitative observation. Particularly as many ecosystems experience unprecedented rate of environmental change, quantitative methods may quickly adapt to community dynamics observed under novel circumstances; shared vegetation responses to extreme drought or disturbance events, for example, may be better distinguished through unsupervised classification than continuous human observation.

Discrete categorization of community states also lends itself an intuitive definition of resilience--the probability than a community retains its state assignment in subsequent observations--that mirrors existing conceptual tools. As a result, direct quantification of resilience across different state types and contexts directly informs restoration and land management efforts. Resilience to change often forms a cornerstone of efforts to adapt to stressors such as climate change, species invasion, and shifting disturbance regimes.

In light of recent climatic extremes influencing California annual grasslands, there is clear need to evaluate existing paradigms of vegetation dynamics used to guide ecosystem management in this system. While many controlled experiments have explored the effects of climatic variation on plant productivity and competition, few have attempted to evaluate how interactions between environmental variation, priority effects, and resilience control long-term patterns of turnover among dominant species groups.

Here, we assess interactions between community assembly and climatic variation on vegetation composition in California annual grasslands across a 10-year period encompassing extreme drought (2013-2016) and potential recovery. Using data from experimental plantings of three key grassland species groups – naturalized annual, native, and invasive species – we aim to test key assumptions of the resilience of different communities and the potential drivers of transition between them.

* What “states” best partition observed variance in plant community composition? What species define these states?
* What states arise with different planting composition mixtures? As these states are observed over time, are transitions between states characterized by continuous, reversible changes or non-reversible changes?
* How do key drivers of community composition (assembly order and climate) govern transitions between states?

**Materials and Methods:**

**Study site**

Field plantings were conducted in research fields at the University of California, Davis (38.545751, -121.784780). Previously used in crop production, these fields were left fallow from 1985 to the start of experimental plantings in 2007. 75% of field is composed of Reiff series soil (coarse-loamy, mixed, superactive, nonacid, thermic Mollic Xerofluvents); other soil present (< 25% of the area) is the Brentwood soil series (fine, smectitic, thermic Typic Haploxerepts) with a 0-2% slope (USDA Web Soil Survey, <http://websoilsurvey.sc.egov.usda.gov>).

In the early fall of 2017, soil was disked, irrigated to stimulate germination of the seedbank, and received a broad-spectrum herbicide (glyphosate) prior to planting to remove the existing seed bank. Three planting mixtures were established based on common delineations between vegetation types in California annual grasslands (Appendix 1). For all possible 1-, 2-, and 3-group planting combinations, we established eight 1.5m x 1.5m plots (2.25 m2; 56 plots total). In each 1.5 x 1.5 m plot, a total of 139 grams of seed was added. This seeding rate reflects an average of 8,000 plants/m2, a typical mature plant density in this system (Heady 1958).

For each monotypic community (e.g. native vs. invasive vs. naturalized), an equal proportion of seeds of each species was added. For community mixtures, an equal proportion of community type seed was added (e.g. in invasive + naturalized, 50% invasive, 50% naturalized seed), with equal proportion of individual species within each community type.

In each growing season from 2008 – 2018, total areal cover of all species was estimated visually to the nearest 10%. Cover observations for each species were performed in mid- and late-spring to capture the season of maximum percent cover for each species, because any one sampling wouldn't account for variation in species phenology.

**State Classification**

Due to intermittent colonization events by agricultural weeds, community analyses were performed on a subset of the total community corresponding to species that were planted in our initial mixes, in addition to *Bromus diandrus*, a common naturalized annual grass that was self-recruited into the experiment during the drought. The resulting dataset captured 93% of the total vegetation abundance observed over the course of the experiment.

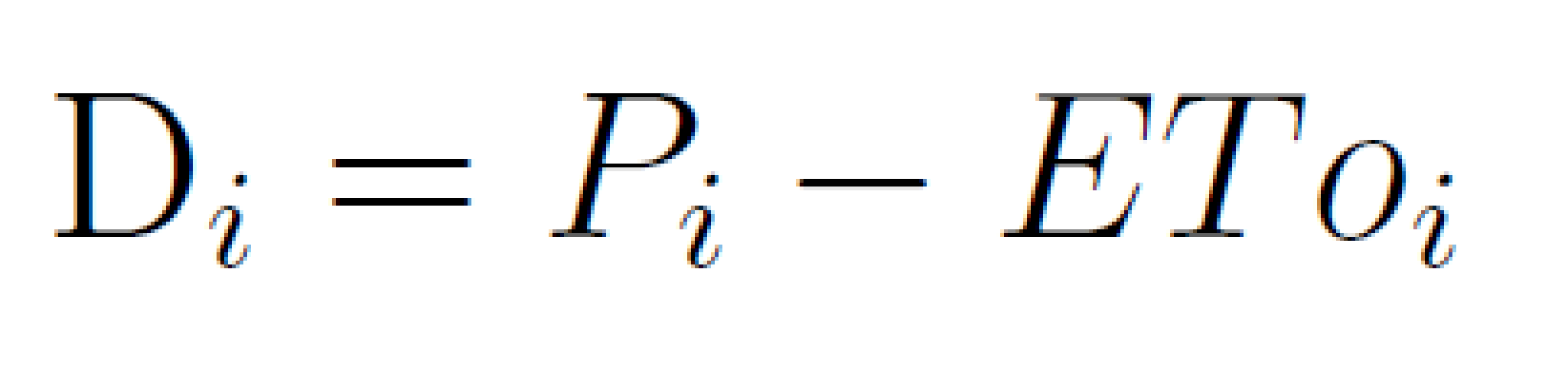
To assign state types to plot observations, we partitioned total community variation into a series of potential states using an unsupervised clustering algorithm, K-medoids clustering. K-medoids clustering randomly selects *k* of *n* total datapoints as group “medoids” and computes the sum of distances between points and their associated medioid, based on Bray-Curtis dissimilarity. This algorithm then iteratively swaps medoids and recalculates summed distance to achieve a solution that best captures the total variance of the data

To determine the most appropriate number of states, we applied k-medoids clustering across values of *k* from 2-10. We then subjected the output of each of these runs to a battery of tests—Hartigan, CH, Beale, KL, Cindex, DB, Silhouette, and Duda indices in the “NbClust” package (Charrad et al. 2014). The value of *k* with the most consistent performance across all tests was used to determine the number of clusters that best represented discrete partitions within this dataset.

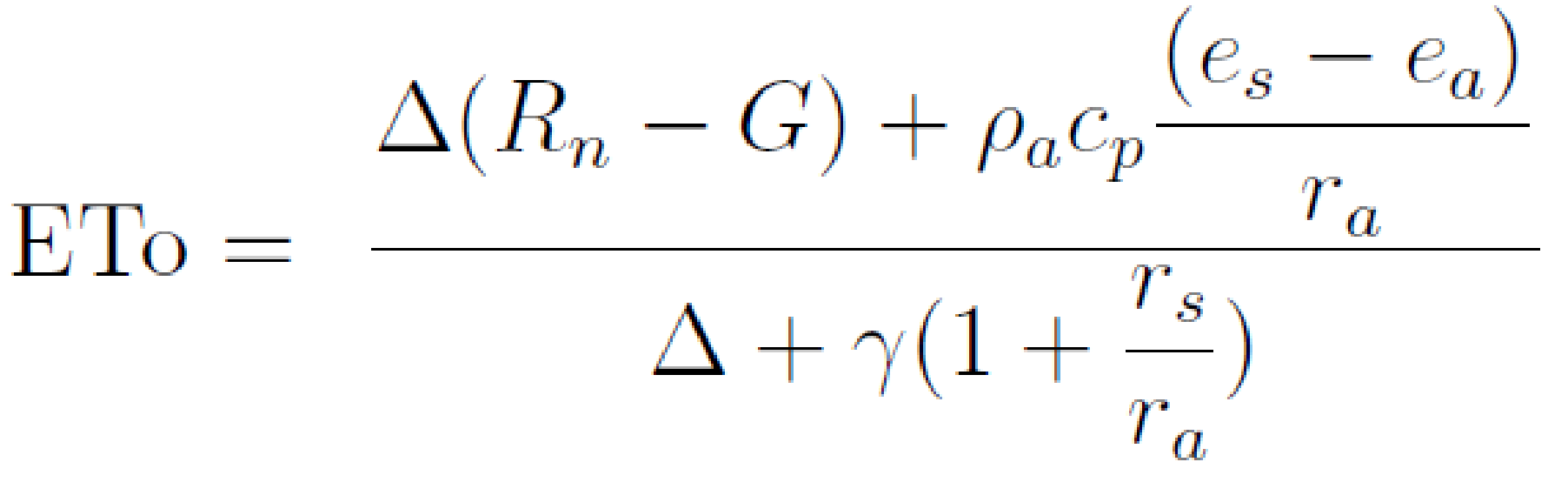
Following the partition of states, we then conducted indicator species analysis to establish what species are associated with each state. Indicator species analysis was performed using the “indicspecies” package in R, using 999 random permutations of state assignments to quantify statistical significance.

**Weather data**

Weather data was provided by a local California Irrigation Management Information System (CIMIS) monitoring station in Davis, CA (38.535694, -121.777636). CIMIS automated dataloggers collect weather data on a minute-by-minute basis, including air temperature, soil temperature, precipitation, solar radiation, vapor pressure, and wind speed. We aggregated these data into monthly intervals, where we calculated Standardized Precipitation-Evapotranspiration Index (SPEI), a metric of drought stress (*D*) at a given timepoint, *i*:



Where *Pi*represents observed precipitation and *EToi*represents estimated evapotransporation. *ETo* was calculated using the Penman-Monteith equation, defined as:



Where *Rn* is net radiation, *G* is soil heat flux, *(es – ea)* isthe vapor pressure deficit of air, *ρi* is the mean air density at constant pressure, *cp* is the specific heat of air, Δ is the slope of the saturation vapor pressure temperature relationship, γ is the psychometric constant, and *rs*and *ra* are the surface and aerodynamic resistances (FAO). SPEI offers flexible, variable timescale estimations of drought stress that can be used to quantify the effects of multi-year climate patterns (Vicente-Serrano et al. 2010).

To provide context for climate patterns observed during our study, we calculated SPEI for a 35-year span between 2018 and 1983, the first year sufficient climate data was collected (Appendix 2). To account for temporally lagged effects of climate variation (Dudney et al. 2017, Prugh et al. 2018), we created drought indices across several cumulative water year durations. For each year, we calculated SPEI for a single water year (October – May; 8 months), two consecutive water years (20 months), and three consecutive water years (32 months). We then standardized these values by fitting the drought index series to a log-logistic distribution, wherein scaled drought indices represent historic droughts (-2) to historic wet periods (+2).

**Construction of Multistate Models**

Following the association of observations to discrete states, we fit a multistate model (syn. Markov model) to the data. Multistate models represent systems where subjects transition between a set of discrete classes over time and may be uniquely suited to expressing state-transition model concepts in a statistical framework.

In multi-state models, transition probabilities between states are modelled as a transition matrix. To explore transitions between states previously identified in clustering, we fit a transition matrix consisting of all possible transition directions, resulting in a base model of (*K-1) \* K*estimated parameters, where *K* is the number of states.

To test for the effects of hypothesized drivers of vegetation turnover, we fit a series of candidate models that also included the influence of planting composition (temporal priority effects) and climate (SPEI) on estimated transition probabilities. Temporal priority was defined as a 1/0 indicator variable of whether the indicator species of a given state were a component of the seeded species mixture.

After fitting models with and without SPEI and initial planting covariates for 1-, 2-, and 3-year drought indices, we calculated AIC scores for each model. We selected the model with the lowest AIC score as our best fit model. Multistate model fitting and model selection was performed using the “msm” package.

**R packages:**

Data were visualized using “ggplot2” and “network”.

SPEI calculations were performed using the package “SPEI”. Clustering and diagnostics were generated using the packages “pam” and “nbclust”.

Indicator species analysis was performed using “vegan”.

Construction of multi-state models was conducted with the package “msm”

All analyses were conducted in R version 3.06.

**Results**

*Partitioning vegetation into discrete states*

K-medoids clustering of community variance observed (*n* = 560) between 2008 – 2018 indicated that *k* = 4 clusters best partitioned plant communities. A battery of heuristics used to determine clustering effectiveness across *k* = 2-8 clusters demonstrated consistent high performance of *k* = 4 discrete plant community types. This cluster number was the best ranked value of *k* across 4 of 8 heuristic measures (Appendix 3).

To establish which species best characterized different community types we conducted indicator species analysis using cluster assignments produced from *k*-medoids clustering.

Three of the resulting clusters exhibited correlated species groups that largely follow established vegetation types within this system (Table 1) – native species (state 1), naturalized annual grasses (state 2), and invasive weeds (state 3). However, a fourth state, primarily characterized by *A. fatua* and *B. diandrus* appears distinct from other naturalized annual grasses.

These cluster assignments were visualized using non-metric multidimensional scaling (NMDS; Figure 1). Species vectors presented are those with significant (p < 0.05) state associations.

*Frequency of states over time*

Relative frequency of state assignments was not uniformly distributed over the course of observations and appear to correlate with interannual climate variation (Figure 2). State 2, characterized by naturalized annual grasses, composed a majority of all community observations following initial planting. Indeed, all seed mixtures containing naturalized grasses received this state assignment, reflecting the early dominance of these species when seeded contemporaneously with competitors. However, this state soon declined in relative frequency as invasive grasses (state 3) proliferated during moderate to high precipitation years after seeding, followed by a dramatic increase in a subset of naturalized annual grasses (state 4) during an historic drought thereafter. All plots exhibited at least one transition over the course of observation, and visual inspection of transition events showed that while seeding treatments appeared to vary in their transition frequency, transition events were largely consistent within seeding groups (Appendix 5).

Simple tracking of transition frequencies constructed from observations of state assignments and transition events indicates that states differed significantly in their resilience -- the probability of retaining a given state assignment in the next year of observation (Figure 3, contingency table presented in Appendix 3). Three state assignments shared roughly similar resilience—states 1, 3, and 4—while state 2 appeared significantly less resilient over the course of our observations.

Transition events also differed significantly between state pairs. Certain transitions between state pairs, such as those between states 1 and 3, exhibited evidence for non-reversible changes – high transition frequency in one direction, yet low transition frequency in the reverse. In other contexts, communities appeared to cycle readily between two different state assignments, such as between states 2 and 4, in which vegetation fluctuates between two different states characterized primarily by naturalized annual grasses.

*Model selection*

However, given temporal variation in state assignment frequencies, it is likely that transition probabilities were not homogenous over the duration of our observation. We fit multi-state models to quantify how two key drivers of state transition, seeding composition and climate, affected the resilience and transition direction of states.

We considered 8 candidate models, including a null model assuming constant transition probabilities between states, and models capturing the cumulative effect of drought stress (SPEI) in 1-3 year intervals and the influence of seeding composition. Comparison of model AIC scores indicated that best fit models included both the influence of seeding composition and climate variation (Table 3). While both 1-year and 3-year cumulative drought stress models provided comparable fits, here we present results from the former due to slightly lower AIC score and greater parsimony. Chi-squared goodness of fit test of this model showed no significant deviations from model assumptions ( = 12, p > 0.20).

*State Transitions*

Multi-state model fitting demonstrated clear influence of temporal priority and drought stress effects on transition probability between states. Under average climatic conditions (SPEI = 0) and without seeding manipulations, states demonstrated a clear hierarchy in resilience, though all states were more likely to retain their state assignment than transition to another (Table 4). As noted previously, State 2 was the least resilient (58% probability of retaining assignment), while state 3 was estimated to be the most resilient state, suggesting that invasive species are able to form resilient communities under average drought stress.

However, we detected significant (*p*  < 0.05) effects of temporal priority and drought stress on a number of transition directions. Transition to state 1, characterized by native perennial grasses, was estimated to be higher for all previous state assignments, ranging from a 2.53- to 12.74-fold increase in the rate of transition to state 1 from other states (Table 4; Figure 4A). Transition events to state 1 were also significantly more likely under wet and dry years when plots were previously given a state 4 or state 3 assignment, respectively; state 3 communities, for example, were roughly half as likely to transition to state 1 per unit increase in SPEI.

Furthermore, states 3 and 4 showed significant changes in resilience in response to climatic variation (Figure 4B). All transitions from state 3 communities appeared highly unlikely in low drought stress years – even when planted alone, particularly wet periods (SPEI = +2) increase the estimated resilience of invasive species to over 90%, while decreasing to below 75% under significant drought (SPEI = -2). In contrast, annual grasses in state 4 appeared most stable under drought conditions, with base transition probabilities ranging from roughly 75% (SPEI = -2) to 65% (SPEI = +2). Together, these results reflect controls of climate and assembly order operating within this system, driving transitions among dominant vegetation types over relatively short (<10 year) timescales.

**Discussion**

Consistent with other characterizations of California annual grassland community dynamics, we observed rapid turnover in dominant vegetation over the course of our study. Through classification of vegetation states and modelling of transition probabilities, we found evidence for distinctions between vegetation types that differed in their resilience and response to temporal priority and climatic variation.

*Partitioning states*

Two identified species groups – dominated by native species and invasive annual grasses – largely followed the divisions made in initial seeding compositions and classic state-transition models of California annual grasslands. However, in contrast to a single state type capturing the abundance of naturalized annual grasses, we found evidence to consider this broad label as two separate vegetation states. This distinction appears to have been driven primarily by the influence of a historic drought event. By emphasizing the difference between annual grass species which dominated many observations early in the experiment and those which increased in relative abundance after the drought, we provide evidence for differences in environmental response. Naturalized exotic annual grasses may exhibit greater variation in response to environmental conditions than often implied by classic state-transition models this system.

This finding demonstrates a key application of unsupervised classification in highly speciose, dynamic systems. Conceptual notions of species “groups” which exhibit correlated fluctuations in abundance often form the basis for exploratory analysis and management action. While keen observers may be able to identify key vegetation types over the long-term, more sensitive quantitative approaches may be better predisposed to capture these correlations when deviating from historical norms.

*Priority and Resilience*

The early abundance of a transient vegetation state dominated by naturalized annual grasses support other observations of naturalized annual grass dominance as effective colonists following disturbance. These species are thought to secure a competitive advantage when given priority in arrival, driven by large seed mass and rapid germination in response to precipitation. While able to secure early advantages during at the seedling stage, this appears to come at a cost of long-term resistance in this system, ultimately giving way to a set of invasive taxa often within two years of initial establishment.

Native perennial grasses, on the other hand, appeared to exhibit a contrasting strategy emphasizing long-term resistance to invasion over colonization ability. Consistent with experiments contrasting performance of native perennial grasses with naturalized and invasive annual grasses, mature bunchgrasses are able to effectively suppress their competitors, yet are often seed-limited (Seabloom 2003) and are poor competitors at the seedling stage; in our experiment, transition events appeared rare when native seeds were not supplied.

Establishment of significant native perennial grass cover is often a key restoration target in California annual grasslands. Our results emphasize the difficulty in assessing the effectiveness of seeding treatments in highly dynamic systems. Just as restoration outcomes may vary considerably between years (Young 2015), short-term observations of community composition may not provide an accurate assessment of treatment success. Particularly for species which exhibit climate-driven fluctuations in relative abundance, successful initial recruitment may lead to subsequent periods of dominance.

*Influence of Climate*

Transitions between two other species groups dominated by invasive and naturalized annual grasses appeared to be controlled largely by interannual climatic variation. The positive responses of these groups in response to wet and dry periods, respectively, emphasizes the role that precipitation patterns play in controlling vegetation turnover within annual grassland communities.

Temporal resource heterogeneity has long been theorized to drive coexistence in annual plant communities. In annual grasslands of California’s central valley, precipitation manipulations have often resulted in increased growth of dominant grass species, particularly those able to effectively utilize residual soil moisture present near the end of the growing season. The two invasive species in our study, medusahead (Taeniatherum caput-medusae) and goatgrass (Aegilops triuncialis), exhibit delayed phenology relative to other annual grasses and thought to beneift from late season precipitation during wet years.

More curious is the apparent affinity to drought conditions among a subset of naturalized annual grasses. In many experimental manipulations, annual grasses are reported to compete less effectively and experience excess mortality during drought conditions. However, germination and seedling survival in California annual grasslands are known to vary strongly both with the timing of quantity of winter precipitation – water years between 2013 and 2016 exhibited pronounced midwinter droughts, rather than uniform decreases in precipitation. Increased drought intensity early in the growing season may have a more pronounced effect on annual grass survival, when seedlings are most vulnerable.

Alternatively, existing paradigms of vegetation responses to climate variation, which often rely on distinctions made between native, naturalized, and exotic species, may prove more nuanced. Naturalized species, which comprise over 20% of California grassland diversity, may exhibit a rich and varied set of life history strategies. While drought may be detrimental to annual grasses, generally, certain species such as *A. fatua* and *B. diandrus* may be able to capitalize on conditions that more significantly disadvantage other taxa.

*Implications for Restoration and Management*

Quantitative approaches to assessing both the diversity and resilience of vegetation types are likely to serve as important compliments to existing management tools. While our study is limited by its climatic scope and seeding patterns, the unique environmental conditions observed over the course of sampling present a unique opportunity to update core predictions based on state-transition models of California annual grasslands. In highly diverse systems where axes of vegetation change are not readily apparent, attempts to distill community variance into a series of discrete state types may provide an effective bridge between scientific study and land management.

As the effects of anthropogenic climate change continue to mount, the Californian climate is forecast to experience increasing variation in temperature and precipitation. In annual grasslands, greater frequency and intensity of drought events may be expected to drive more rapid fluctuations in plant communities; the resulting challenges to restoration and land management underscore the value of accurate predictions of vegetation change. The analytical framework used here is highly adaptable to many systems and may yield valuable insights into the mechanisms that govern plant community turnover and coexistence, as well as key patterns of resilience and direction of change that form the basis of many land management paradigms.

*Future Directions*

While able to capture the immediate effects of a historic drought on grassland plant communities, the 10-year scope of our study may not be sufficient to accurately assess long-term changes to vegetation dynamics. In particular, we are unable to determine whether the naturalized annual grasses which proliferated following the drought will become less frequent as drought stress decreases. While vegetation may be expected to fluctuate between groups under normal conditions, extreme disturbance events may act as critical tipping points that permanently alter ecosystem functioning.

The observed patterns in our study are also likely to be mediated by the local species pool and experimental community assembly. Given the known effects of temporal priority on vegetation turnover in California, greater variation in assembly order may lead to different definitions of state types and estimated influence of timing in seed arrival. In grassland systems, effects of species richness on invasion resistance have been observed to be non-additive in many contexts; more or less diverse planting mixtures may produce significant changes in state resilience.

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